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CROSSING-OVER AND THE THEORY THAT THE GENES ARE ARRANGED IN THE CHROMOSOMES IN SERIAL ORDER

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In the only organism adequately studied (the fruit-fly Drosophila investigated by Morgan and his associates) the diverse cross-over ratios between different pairs of genes show among themselves a complex system of remarkable relations; it is this system that any theory must explain. The nature of the system is illustrated in table I.

TABLE I

Table of Best-Known Cross-Over Ratios among Genes of Chromosome I of Drosophila, Arranged in Series with Reference to that Gene Having the Highest Mean Ratios (Yellow)

	YELLOW	WHITE	BIFID	CLUB	VERMIL.	MINIAT.	SABLE	RUDIMEN.	BAR
Yellow	—	1.1	5.5	17.7	34.5	34.3	42.9	42.9	47.9
White	1.1	—	5.3	14.3	30.5	33.2	41.2	42.4	43.6
Bifid	5.5	5.3	—	?	31.1	30.6	?	42.7	?
Club	17.7	14.3	?	—	18.8	?	?	?	?
Vermilion	34.5	30.5	31.1	18.8	—	3.1	10.1	24.1	23.9
Miniature	34.3	33.2	30.6	?	3.1	—	6.7	17.9	20.5
Sable	42.9	41.2	?	?	10.1	6.7	—	14.3	13.8
Rudimentary	42.9	42.4	42.7	?	24.1	17.9	14.3	—	2.3
Bar	47.9	43.6	?	?	23.9	20.5	13.8	2.3	—

The peculiarities of this system may be formulated briefly in the following 17 basic propositions.

Basic Propositions—1. The ratios vary from below $^1/_2$ per cent to about fifty per cent. (Ratios as low as .4 per cent have been recorded.)

2. If two genes show with one another a low cross-over ratio, they show nearly the same ratio, low or high, with any other gene.

3. If two genes have together a high ratio (as do Yellow and Bar), their ratios with particular other genes are very diverse.

4. The greater the ratio of two genes together, on the whole the more diverse their ratios with given other genes.

5. If any two genes, *A* and *B*, have together a certain ratio, and *B* has with a third gene *C* a certain ratio, then the ratio of the first (*A*) with the third (*C*) is either a little *less* than the *sum* of the ratios *A* — *B* and *B* — *C*, or a little *more* than their *difference*.

6. If for the gene having the highest mean ratio, as Yellow, we arrange in ascending order the series of its ratio with the other genes,—allowing the position of all the genes to be thus determined,—then all the ratios fall into a systematic table (as table I), having the following characteristics:

7. Genes having a *low* ratio with this basic gene (e.g., White) show with the others a similar ascending series of ratios, but with each ratio slightly *less*.

8. A gene having a higher ratio with this basic gene shows a similar ascending series of ratios with genes having a still higher ratio than its own with the basic gene (though with the ratios much decreased in value):

9. But a *reverse* series with all the genes having a lower ratio than its own with this basic gene. (Cf. the ratios of *Vermilion* with others.)

10. In a table so arranged, if in any column (or row) we take for a gene *A* its two ratios, with *B* and with *C*, these lying on the opposite sides of the diagonal, then the *sum* of these two ratios gives approximately, but somewhat *more* than, the ratio between *B* and *C*. The difference between the sum and the ratio *B-C* becomes greater as *B* and *C* are farther apart in the table.

11. But if *B* and *C* are so chosen that the ratios *A-B* and *A-C* lie on the same side of the diagonal, then the *difference* between *A-B* and *A-C* is approximately, but a little *less* than, the ratio *B-C*.

To these relations, evident from the table, must be added certain others that have been established by experiment:

12. When there occurs a cross-over between any two genes of the series (shown in the upper row of table I), there occurs also as a rule a cross-over between any gene lying to the right of these two and any other lying to the left of these two. Thus, if there occurs a cross-over between Vermilion and Sable, as a rule there occurs also a cross-over between Club and Sable, Club and Rudimentary, Club and Bar, White and Sable, White and Bar, etc., etc.

13. But in such a case there is as a rule no cross-over between two genes in the series on the same side of the two genes that show a cross-over. Thus, if there is a cross-over between Vermilion and Sable, there

is as a rule no cross-over between any of the genes Yellow—White—Bifid—Club—Vermilion; these all remain in the same grouping as before.

14. That is, such series as are represented in the rows or columns of table I usually in crossing-over separate into two groups at a certain place in the series, all the members of one group showing a cross-over with all the members of the other.

15. But in relatively rare cases, such a series separates at two points in the series; in such a way that all the genes between the two points show cross-overs with all the genes outside the two points. Still more rarely, the series separates at three points.

16. In a considerable proportion of the cases (about 30 to 50%) no crossing-over occurs between any of the genes of the chromosome.

17. When a cross-over occurs between two genes *A* and *B* having together a low ratio, no cross-over occurs betweeen one of these genes (as *A*), and any other gene *C* having a low ratio with *A* and lying in the series on the opposite side of *A* from *B*. Or: Such a series as that of Table I does not break at two points that are close together ("Interference").

These relations are shown not alone for the 9 genes given in our table. If we take the other genes of the X-chromosome, they fall, as far as the data on them go, into this same system. Or if we select the most thoroughly studied genes of the second chromosome of Drosophila, and arrange them in a similar way, we find that they yield a table similar to table I, and the propositions set forth above apply equally to them.

Any correct theory of crossing-over must require and account for this system of relations; and also for the particular numerical values in which it is embodied.

The so-called linear theory holds that the genes are arranged in the chromosome in serial order, like the beads on a string. Two such strings lie side by side or intertwine in the known pairing of the chromosomes; crossing-over is held to be due to the fact that at times the strings break and interchange parts,—a portion of one string uniting with a portion of the other to form a new string. Genes farther apart in the strings will be separated by breaks more frequently, it is held, than genes closer together: hence arise the diverse ratios of crossing-over.

This set of conditions would necessarily give rise to a definite set of relations between the ratios. This paper investigates whether this system would be identical with that observed in nature (formulated in the above 17 basic propositions). We deal first with the possible case that a break at any point does not affect the occurrence of a break at any other point. ("No interference.")

No Interference.—Two genes originally in the same chromosome will be separated into diverse chromosomes (and vice versa) when an odd number of breaks and interchanges intervene between them: not when an

even number intervene. Hence the cross-over ratio, C, between any two genes will be the proportion of cases in which there is an odd number of breaks intervening in that part of the chromosome lying between them.

If we let n equal the number of joints intervening between any two genes (as A — H), and if b is the frequency of a break at any joint, it can be shown that the proportion of cases with odd numbers of breaks between these two genes, and hence the cross-over ratio C, is given by the formula:

$$C = \frac{1}{2}\left(1-(1-2b)^n\right) \qquad (1)$$

And from this it can be shown that the number of joints n required to produce any cross-over ratio C is

$$n = \frac{\log. 1 - 2C}{\log. 1 - 2b} \qquad (2)$$

When n is 1, obviously $C = b$; that is, the cross-over ratio between two adjacent genes is b. It follows that b must in nature be less than .005, since cross-over ratios lower than this occur; and that in given cases, n must be sufficiently large to produce the observed ratios from so small a value of b, in accordance with formula (1).

If we take as our unit of length, not the absolute number of joints, n, but a length (number of joints) just sufficient to give 1 per cent of crossing-over (as is done by Morgan and associates), then if we let U be any given number of units, it can be shown that

$$C = \frac{1}{2}\left(1 - .98^U\right). \qquad (3)$$

And the number of units necessary to produce any ratio C is

$$U = \frac{\log.(1 - 2C)}{\log. .98}. \qquad (4)$$

Further, the cross-over ratio C yielded by the sum of a number of stretches having respectively the ratios C_1, C_2, C_3, etc., is:

$$C = \frac{1}{2}\left[1 - (1 - 2C_1)\,(1 - 2C_2)\,(1 - 2C_3)\text{ etc.}\right]. \qquad (5)$$

As to the number of breaks intervening in the stretch between any two genes for any ratio C, it can be shown that, in consequence of the smallness of b and the correlatively large value of n, the proportion of cases B_0, having no breaks is

$$B_0 = \sqrt{1 - 2C} \qquad (6)$$

And the proportion B_d with any other number of breaks d is

$$B_d = \frac{(-\text{Nat. log. } 1 - 2C)^d}{2^d} \frac{\sqrt{1 - 2C}}{d!}. \qquad (7)$$

By the aid of these formulae, the cross-over ratios required by the linear theory without interference may be computed, and their necessary interrelations discovered and compared with those found in nature. When this is done it is found that they yield the entire system of general relations exemplified in table I and formulated in the 17 Basic Propositions above, except the last one (that for which the hypothesis of interference has been proposed). But besides this exception, three important numerical discrepancies are found to exist between the conditions required by the linear theory without interference, and those observed in nature. These are:

(*a*) The observed numerical values of the ratios could not occur: the observed ratios for distant genes are regularly greater in proportion to those for genes close together than they could be on the linear theory without interference.

(*b*) The proportions of the chromosomes showing the different numbers of breaks (0, 1, 2, 3, etc.) are not what are required; there is a marked excess in the proportion showing only one break, and a corresponding deficiency in the proportion showing 2, 3 or more breaks.

(*c*) The "map distances" of the genes, that have been determined for the chromosomes of Drosophila by Morgan and associates are much less than are required by the linear theory without interference.

Thus the linear theory without interference, in spite of the fact that it yields all but one of the *general* relations found in nature, cannot account for the observed ratios and their precise relations.

The Linear Theory with Interference.—To account for the fact set forth in proposition 17, page 143, the hypothesis of interference has been proposed. This assumes that the occurrence of a break at a certain joint in the linear series of genes interferes in some way with the occurrence of another break at any joint within a certain distance.

If valid, the hypothesis of interference must preserve intact the validity of propositions 1 to 16, pages 141–143; and it must not only account for proposition 17, for which it was devised, but it must also do away with the three discrepancies just mentioned, for which it was not devised. To determine whether it can meet this severe test, mathematical formulae must be developed for crossing-over with any extent of interference.

The value of the cross-over ratio C, in case of interference extending over a certain percentage P is the sum of the proportions $B_1 + B_3 + B_5$, etc. having the different possible odd numbers of breaks intervening between the two genes in question. If we let $A = 1 - P$, and $m =$ a factor by which P must be multiplied to give the number of units between

the genes, then it is found that the proportions having the different numbers of breaks are as follows:

The proportion B_0, having no breaks is, in case of interference:

$$B_0 = A^m. \tag{8}$$

The proportion B_1 with just one break is

$$B_1 = A^{m-1} P + (m - 1) A^{m-1} (-\text{nat. log. } A). \tag{9}$$

And the proportion Bd with any required number of breaks d is

$$B_d = (-\text{Nat. log. } A)^d \left[\frac{(m - d + 1)^d - (m - d)^d}{d!} A^{\frac{2m - 2d + 1}{2}} + \frac{(m - d)^d}{d!} A^{m-d} \right]. \tag{10}$$

The cross-over ratio C is

$$C = B_1 + B_3 + B_5, \text{ etc.} \tag{11}$$

Practically it will be found that the value of B_d when d is greater than 4 is negligible, except for the working out of theoretical cases in which the distance over which interference extends is very great and the length of the chromosomal stretch is many times this distance.

By the aid of these formulae (8) to (11) the cross-over ratios for various extents of interference may be computed and their system of relations determined and compared with those found in nature. When this is done, the following are found to be the facts.

(*a*) Crossing-over in the manner required by the linear theory, with interference extending on the average to a distance itself yielding about 20 to 25% crossing-over, shows and requires all the general relations set forth in propositions 1 to 17, as characteristic of the relations found in nature.

(*b*) It also requires and accounts for the conditions giving rise to the three numerical discrepancies (*a*), (*b*) and (*c*), set forth on page 145 as existing between the conditions found in nature and those required by linear crossing-over without interference. With interference of 20 to 25% these discrepancies disappear.

Thus in sum the linear theory of crossing-over, with interference of 20 to 25% gives the entire system of complex and peculiar relations found in nature (set forth in the 17 propositions of pages 141–143) and at the same time requires and accounts for the specific numerical data—the relative ratios of different genes, the "map distances," and the relative proportions of chromosomes showing 0, 1, 2, 3 or more breaks.

No other theory that has been suggested yields any such system. In view of the complexity and marked character of this system, and in view of the precise numerical proportions it involves, it is difficult to conceive that any other set of conditions than that set forth in the "linear theory" could produce it.

The complete paper, with derivation of the formulae and detailed comparison of their requirements with the conditions found in experimental breeding, will appear in *Genetics*.

SOME CONSEQUENCES OF DIFFERENT EXTENTS OF INTERFERENCE, IN THE CROSSING-OVER OF THE GENES

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In the paper which precedes this, it is shown that if the genes at the time of crossing-over are arranged in a linear series, and crossing-over occurs by breaks and exchanges between the two paired chromosomes, then the entire complex system of relations shown in nature by the cross-over ratios is required and accounted for, even in its numerical details; provided that a break at one point interferes with another break within a distance that, on the average, yields a 20 to 25% cross-over ratio.

But if interference extends over a distance distinctly greater or less than this amount, the system found in nature is not produced. In the case of no interference, as shown in the previous paper, the divergences from the natural system are not very great. If interference extends to 30% ("30 units") all the general relations found in the natural system are retained, but the numerical values show discrepancies.

But with interference extending beyond 30 units, the system changes greatly. Below that value, no cross-over ratios exceeding 50% are produced, and the greater the distance between two genes the greater the cross-over ratios between them.

If now by the aid of formulae (8) to (11) of the preceding paper, we determine the system of cross-over ratios for a series of interference values, from 30 units up to say 90 units, we find that the cross-over ratios show the values indicated by the curve of figure 1. With interference above 30 units, the cross-over ratios rise, as the genes are made farther apart, above 50%. Thirty-five units' interference yields a maximum ratio of 52.4%; 50 units, 60.6%; 75 units, 77.9%, 90 units, 90%, and so on.

After the maximum is attained, if the distance between the genes is still farther increased, the cross-over ratio begins to decrease, falling again

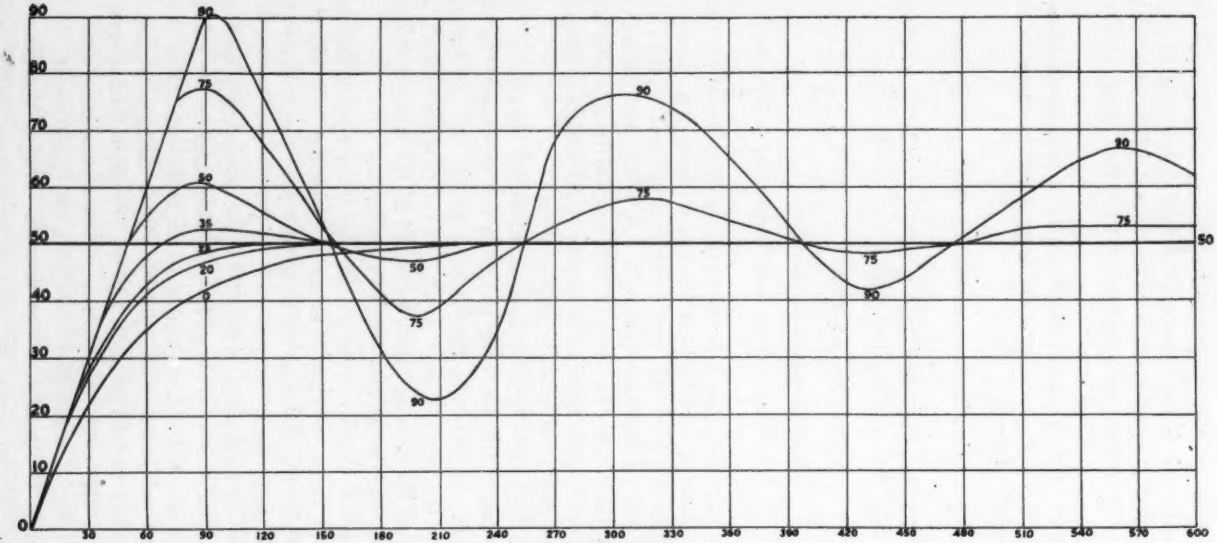

FIGURE 1

Curves showing for a number of different amounts of interference the changes in the cross-over ratios as the distance between the genes increases. The vertical scale gives the cross-over ratios, in percentages. The horizontal scale gives the distances apart of the genes, in standard units (each unit being a distance sufficient to give 1% of the crossing-over). The figures on the curves show the amount of interference represented by that curve. The curves for no interference and for interference extending 20 to 25 units do not rise above 50%; those for 35, 50, 75 and 90 units rise above 50%, descend as the distance between the genes becomes greater, and oscillate below and above 59%, as shown.

below 50%. At a still greater distance it rises again, thus undergoing oscillatory changes above and below 50%. With increase of distance the oscillations become less marked, until at a sufficiently great distance the cross-over ratio settles down at 50% (or in close approximation to that value).

Obviously, for interference extending over long distances, the serial order of the genes would not be given by the increasing values of the cross-over ratios with the end genes. Genes farther from the end would often have a lower cross-over ratio with it than genes nearer to it. Chromosome maps constituted, like those in use in Drosophila, on the basis that increased ratios mean greater distances, would give incorrect and inconsistent results. However, maps showing the correct order of the genes could still be constructed by considering successively genes having cross-over ratios less than the number of units of interference.

Cross-over ratios above 50% have not thus far been certainly found in nature. If such should be found, a high degree of interference is indicated, and it is to be anticipated that there will occur also the other relations shown in this paper to accompany high interference.

Details are given in a paper to be published in *Genetics*.

GENETIC VARIATION IN LINKAGE VALUES[1]

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In a recent paper[2] in these PROCEEDINGS, the senior writer reported briefly on several independent series of selection experiments with Drosophila melanogaster, in which the cross-over value for red eye and long wing (vs. white eye and miniature wing) was gradually and yet markedly reduced. Each series began with a single pair showing the usual cross-over value (about 33%) characteristic of the so-called normal population. Series A, and its derivative, A′, were reduced to practically 0% in about ten generations, but were not carried beyond the F_{15}. Series B was reduced to about 5–6% crossing-over in 29 generations and has bred relatively true for over sixty generations. When Series B was crossed to normal, white, miniature individuals, the results of the F_1 and F_2 bore the distinctive features of *multiple factor* inheritance; and from these results I ventured to conclude "the hybridization experiments indicate that the amount of crossing-over is at least markedly influenced, if indeed it is not actually determined by multiple factors." Without quoting anyone, directly, I questioned furthermore, "the current view that 'the

percentage of cases in which two linked genes separate (amount of crossing-over between them) is necessarily proportional to the distance between these genes, other things being equal,' i.e., under ordinary circumstances and in the absence of unusual factors or environmental conditions which geneticists recognize." (The secondary quotation had been taken almost directly from Weinstein ('18),[3] who also adds pertinent reservations.)

In a more recent paper in these PROCEEDINGS, Sturtevant ('21)[4] commented briefly on the essential elements of my study, but stressed with detailed references and quotations that which I had thought unnecessary to particularize, viz.: that geneticists have recognized the existence of unit factors and environmental conditions which effect crossing-over. Sturtevant states, "One unfamiliar with the literature of the subject would probably infer from Detlefsen's paper that the possibility of inherited linkage variations had not been taken into account by those concerned in constructing chromosome maps." I had rather expected that the *last quotation in the foregoing paragraph, taken directly from my former paper,* would make the facts quite clear to those familiar or even unfamiliar with the literature on this subject, for I had stated specifically that geneticists had recognized both factors and environmental conditions which influence crossing-over. Therefore, it seemed unnecessary to encumber a preliminary account with detailed references, since I was not dealing with a new and unusual single genetic factor such as those described by Sturtevant ('19)[5] but perhaps with a group of modifiers which appeared to exist in any ordinary Drosophila population and which were simply sifted out by selection,—at least as far as I have been able to discover up to the present time. Sturtevant also added that "chromosome maps are intended to show the actual sequence of the loci and the relative amounts of crossing-over between them." In other words, chromosome maps are not maps literally but simple graphs of linkage values showing the order of genes, and there should be no confusion as to the relationship between such graphs and the actual chromosomes. This conservative position has been suggested and maintained by some investigators and these simple facts are quite familiar to those following these important researches, notwithstanding Sturtevant's concluding sentences: "In view of these considerations it is clear that Detlefsen has misunderstood the significance of the published maps. The conception he has attacked has not been held or urged by those who have constructed chromosome maps." But as Sturtevant ('19)[6] himself admitted "the terms, distance and crossing-over, have unfortunately been sometimes used almost as though synonymous and confusion has perhaps resulted." Sturtevant ('21)[7] stated later, "It has been found possible to determine the linear order of the genes within any one chromosome pair, and to obtain a measure of their distance

apart. On the basis of this information, when the position of a new gene has been determined with respect to any two others in its group, it is possible to predict accurately, the relations that it will show to any other genes." It is precisely the meaning, accuracy, and reliability of this "measure of their distance apart" which constitute legitimate questions for investigation. As far as I am aware, we do not possess complete information on these points yet, and perhaps some of the more popular presentations and conclusions at least have outstripped, in their implications, the demonstrable evidence. This current viewpoint is well stated by Punnett ('19)[8] and Walter ('22).[9] (Cnf. Babcock and Clausen ('18),[10] p. 116 et seq.; Nachtsheim ('19),[11] p. 140 et seq.; Sharp ('21),[12] p. 386 et seq.; et al.).

Sturtevant drew attention to the well known fact "that definite evidence for the existence of genes modifying the amount of crossing-over was reported. . . .;" but no reference which Sturtevant gave dealt with multiple modifying genes sifted out of a general population by selection, *nor was any alternative explanation offered for the results of my experiments.* The chief difference between Sturtevant's cases and mine lies in the fact that the former seemed to involve a *single* modifying gene encountered quite unexpectedly, while the latter followed a deliberate attempt to modify a linkage relationship, and the subsequent genetic tests bear the ear-marks of *multiple* modifying genes. Whatever differences of view or opinion may exist, we are quite agreed in recognizing the importance of any facts which may perhaps throw additional light on the phenomenon of crossing-over, all phases of which are by no means completely understood. With this in mind, some additional genetic tests of our low cross-over stock were made to ascertain if possible (1) whether the reduction in amount of crossing-over had been equally effective on cross-over values between genes supposedly and probably lying inside of the original region of selection, (2) whether cross-over values outside of the region of selection had likewise been influenced, and (3) whether the different regions of the chromosome would show a blend in cross-over value in the F_1 and F_2, and an increased variability in the F_2. For this purpose, two special stocks were made up: the first, a 4-point stock, having four mutant genes, white eye, crossveinless, cut, miniature wing; and the second, a 5-point stock, quite similar except that it had forked bristles in addition.[13] For the sake of brevity, I shall refer to the regions between the mutant genes as regions 1, 2, 3 and 4, reading from white to forked on the graph of linkage values. The average linkage relationships in normal stock using large numbers are about as follows:

White.....crossveinless.....cut.....miniature.....forked

Region 1 = 12.2% region 2 = 6.3% region 3 = 16.1% region 4 = 20.4%

Two females of the F_{69} Series B were mated individually—each one to a normal 4-point male. They showed 5.84% cross-overs in 291 offspring, the approximate value in our low cross-over stock. Two males of the F_{69} Series B were mated, each one to a normal 4-point female. Twenty-one quadruple-heterozygous F_1 females from these four crosses were then back-crossed to the ultimate recessive 4-point stock, each female being bred exhaustively. In addition, a single random male from the F_{74} Series B was mated to a normal 5-point female. Eighteen F_1 and twenty-two F_2 quintuple-heterozygous females were bred exhaustively to 5-point males. The results of the 4-point crosses and the 5-point cross all agree with each other sufficiently well to justify pooling the data for the present discussion. For this purpose, table 1 has been constructed. The cross-over value of each female for a given region based on her long winged progeny was treated as a variate and classified in a frequency distribution with class intervals of 0.5% for regions 1 and 2, and 1% and 2% for regions 3 and 4 respectively. The cross-over value of each female based on her total progeny was similarly treated.

This separate treatment of long winged classes was attempted in order to eliminate, as far as possible, the effects of differential viability in the complementary miniature classes. Combining all classes in the totals, however, does not materially alter the general conclusions, although it gives in every case, but one, a slight increase in cross-over values, for the obvious reason—the miniature parental class (non-cross-over) is the least viable. The very large number of offspring per variate, perhaps in part due to heterosis, gives more confidence in the cross-over values of such individual variates—over 650 offspring per female in the F_1 and F_2 of the combined crosses, and 709 in the F_1 of the 5-point cross.

The data of table I answer our three stated questions as follows:

(1) The reduction in amount of crossing-over was not equally effective on cross-over values in the different regions lying inside of the original field of selection. Basing our conclusions on the more reliable long winged classes, the F_1 shows 17.7%, 31.3%, and 39.9% of the normal crossing-over in regions 1, 2, and 3, respectively. Reduction had therefore been most effective at the left end of the graph and the effectiveness apparently decreased progressively in regions to the right. If we draw our conclusions from the miniature classes or total data, they are not materially changed.

(2) Region 4, outside of the original field of selection, shows 14.22% crossing over in the F_1 which is 69.7% of the normal amount—a significant difference.

(3) In the F_1 and F_2, each region without exception, shows a cross-over value lower than that of the normal population, as indicated by the mean variate or mean total crossing-over. Furthermore, the F_2 values for both constants, are consistently higher than the F_1 in every

region. In each region, the variability, as measured by the standard deviation, is increased in the F_2.

The consistent increase in the percentage of cross-overs of the F_2 implies in itself some degree of dominance of low crossing-over. We cannot know the approximate cross-over value of the low parent for each region, since this stock was heterozygous for white and miniature alone, but if the F_1 value for any region were above the mean of the two parent stocks, the F_2 cross-over value would be *decreased* (with the reappearance of the lower F_2 segregates) when the complex of causes acts in the usual Mendelian fashion hypothecated in cases of multiple factors with incomplete dominance. But the F_1 and F_2 value would be alike in these crosses if a definite gene for low crossing-over were located in the sex chromosome itself. However neither event occurs and it appears that low crossing-over acts as if partially dominant in every region. Consistent with this is the actual *rise* seen in each one of the sixteen F_2 values for crossing-over. In fact if the F_1 values in regions 1, 2 and 3 were greater than (or even equal to) a mean between low and normal, the most elementary principle of a conditional inequality would indicate that the cross-over value of the low parent in each region was less than zero—which seems absurd and is therefore ruled out.

The differences between the means of the F_1 and the F_2 are more than merely suggestive, for they not only appear consistently but they are significant in view of their probable errors, which were calculated but are not given. The same is likewise true of the differences in percentage of cross-overs in the F_1 and F_2; and we may apply the theory of errors with reasonable safety in these cases, for although $p-q$ is large, n is also very large, and $p-q$ is relatively small compared with $\sqrt{npq}$.

Table I shows that the mean total crossing-over is slightly higher than the mean variate in fifteen out of sixteen cases (F_2 total, region 3 is an exception). The difference is not great and probably represents a slight tendency to positive correlation between percentage of cross-overs and total progeny, such as Gowen ('19)[14] reported for chromosome III—since calculating the percentage of cross-overs gives a weighted mean, and the more numerous progeny of the higher variates would tend to increase this value over that obtained by treating each female as a single variate in a frequency distribution.

As stated, a rise in the mean value of the F_2 should accompany partial dominance of low crossing-over, and with this, we should find an increased variability in cross-over values in the F_2. Each one of the four regions, using either the more reliable long-winged classes or the total classes, shows such an increased dispersion in the F_2 as measured by the standard deviation. These differences in variability between the F_1 and F_2 appear consistently and are significantly large in every case except in region 4.

TABLE I

The Frequency Distributions of Cross-over Values in the F_1 and F_2 of a 4-point and 5-point Cross between Low Cross-over Stock and Normal

REGION AND NORMAL VALUE	CLASSES	NUMBER OF VARIATES	DISTRIBUTION OF CROSS-OVER VALUES																		MEAN VARIATE	σ	CROSS-OVERS	TOTAL	% OF CROSS-OVERS	AVERAGE NUMBER OF OFFSPRING PER PARENT
			0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75	7.25	7.75	8.25							
	F_1 long	39	2	3	4	11	7	5	3	3	1										2.10	0.96	326	15085	2.16	386.8
	F_2 long	22	2	1	1	1	2		2	1	1	4	1	2	2		1	1			3.93	2.17	310	7704	4.02	350.2
1	F_1 total	39	1	3	7	8	7	7	3	2	1										2.10	0.91	567	25909	2.19	664.3
12.2%	F_2 total	22	1	1	1	1	3		1	1	2	2	2	4			2			1	4.18	2.15	614	14365	4.27	653.0
	F_1 long	39	2	3	8	15	4	2	1	4											1.84	0.88	297	15085	1.97	386.8
	F_2 long	22	1		2		1	4	3	3	3	1	1	1			1	1			3.66	1.76	303	7704	3.93	350.2
2	F_1 total	39		4	7	11	7	6	2	1		1									2.01	0.85	553	25909	2.13	664.3
6.3%	F_2 total	22			1	1	3	1	2	3	4	1	3	1	1	1					3.93	1.44	566	14365	3.94	653.0
			2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17								
	F_1 long	39	1	3	3	8	6	8	4	5		1									6.23	1.99	970	15085	6.43	386.8
	F_2 long	22				1	2	1	3		2		5	3		3		2			11.18	3.49	865	7704	11.23	350.2
3	F_1 total	39		1	1	8	6	5	6	6	3		2	1							7.36	2.27	1979	25909	7.64	664.3
16.1%	F_2 total	22						1	2	2	1		4	4	5	2	1				12.14	2.49	1739	14365	12.11	653.0
			9	11	13	15	17	19	21	23	25															
	F_1 long	18	1	4	5	4	2	1	1												14.00	3.00	999	7024	14.22	390.2
	F_2 long	22		2	2	3	3	8	3		1										17.45	3.41	1374	7708	17.83	350.4
4	F_1 total	18	1	1	7	6	1	2													14.22	2.42	1845	12758	14.46	708.8
20.4%	F_2 total	22		1	3	3	4	8	1	2											17.36	3.11	2585	14572	17.74	662.4

There can be but little doubt, however, that region 4 shows modifications and differences since the means of the F_1 and F_2 and normal are significantly different. The consistent increase in the standard deviation of the F_2 corroborates our previous results on the region from red to long and points to segregation and recombination of genetic factors for crossing-over.

Crossing-over is evidently an enormously variable phenomenon in Drosophila melanogaster, as Gowen found in the third chromosome and as I have experienced in the sex chromosome. Even at the end of 28 generations of close inbreeeding and selection, the relative variability remains extremely high. The mean crossing-over was modified in several independent series, A, B, C, and D; and in a series E, derived from a cross between B and a normal population. The junior writer was assigned the problem of selecting for reduction of cross-over values in the region from miniature to non-bar, neglecting the region to the left. This series, D, began with a single pair chosen at random and was unrelated to former series. The details of the experiment will, I hope, be published later; but a preliminary statement is to the point. Although the left hand region was in this case outside of the field of selection, it was apparently affected to a greater extent; for a cross between series D and a 5-point stock showed 16.96% for the region from miniature to non-bar, and 8.01% for the region from white to crossveinless—the results based upon over 12,000 F_2 offspring. It appears that the chromosome responds as a whole, but perhaps with characteristic changes in exchange value at different levels. Just why this should be so, I do not know; but the phenomenon justifies additional research into the more remote causes. It remains to be proven that the cross-over value in the progeny of any "normal" pair chosen at random cannot be easily modified, particularly in specific regions of a chromosome.

In series B, the left end of the graph of linkage values shows the greatest effect, while regions to the right show gradually decreasing effects, including region 4 which lay outside of the original field of selection. The variability in every region was increased in the F_2 in a cross between normal and low stock. Obvious explanations suggest themselves; and although, at best, they are only tentative and may bear little or no relation to the real facts, they serve as suggestions for future tests to determine the value of alternative hypotheses. Since each independently repeated experience has given a modified cross-over value, it would appear that numerous modifiers are isolated which exist in any normal stock; or that new mutant "genes" modifying exchange arise easily; or that the physical basis of exchange, whatever it may be, is not extremely stable but rather readily modified.

[1] The data were collected by both authors at the College of Agriculture, University of Illinois. The senior author is alone responsible for the manuscript and any views or shortcomings it may contain.

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THE DISPLACEMENTS OF THE CAPILLARY ELECTROMETER, FOR PROGRESSIVE DILUTIONS OF THE ELECTROLYTE

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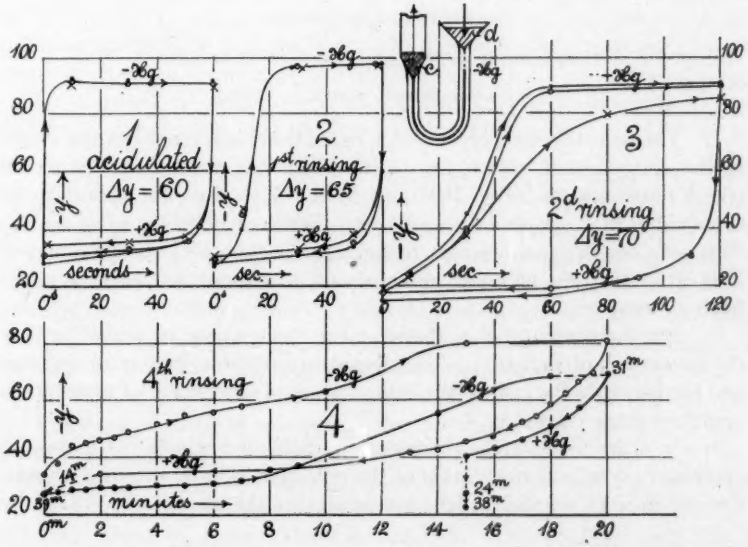
1. The attached graphs, obtained incidentally, seem to be of sufficient interest to be recorded. The capillary electrometer is shown in diagram in the inset, the mercury thread being about 1 mm. in diameter. The meniscus below d is in contact with the electrolyte, while a platinum wire dips into the broad meniscus at c, so that but one meniscus is in question. The displacements were observed with a microscope provided with an ocular scale, of which 1 scalepart y corresponded to .041 mm. of depression, at the meniscus. They are recorded as observed with an *inversion*, so that a rise of meniscus corresponding to a + charge happens to be laid off downward and a depression of meniscus (negative charge) upward. The ordinates therefore are $-y$. One ($ZnSO_4$) Daniell cell and a commutator were used for charging, the electrodes being alternately earthed.

2. In the graphs, figure 1, the electrolyte (inset d) was distilled water, to which a drop of dilute sulphuric acid had previously been added and mixed. The observations were made in seconds, after closing and after opening, the cycles given (points distinguished) are the 4th, 5th, and 6th. The equivalent of the Daniell cell is here about $\Delta y = 60$ scaleparts.

3. The whole of the electrolyte in d was now removed and replaced by distilled water, the mercury thread being left in place. The three new cycles, figure 2, show a somewhat enhanced displacement, Δy; but the feature of the results is the much more rapid displacement of the negative meniscus, as compared with the positive meniscus. Graphs in the latter case are always doubly inflected; not so in the former.

4. The electrolyte was now again removed and replaced by distilled water. The cycles obtained after this second rinsing are shown in figure 3. There has been further and now very marked retardation of the whole



phenomenon; nevertheless the discharge of the negative surface is still strikingly rapid as compared with the discharge of the positive surface. The total displacement Δy is possibly larger than before.

5. Correspondingly progressive results were obtained in the 3rd rinsing. I shall therefore only give the record for the 4th rinsing, in figure 4. The phenomenon has now been so far retarded, that a time scale of *minutes* is necessary. Even this does not suffice, so that the long intervals are indicated by broken lines. The supply of ions (presumably proportional to the fall of potential per second) is now very meager; still the mercury surface parts with its positive ions appreciably more reluctantly than with its negative ions, and the latter graphs, as heretofore, are not doubly

inflected. All this fits in very well with the theory of Helmholtz and Lippmann based on the 2nd law of thermodynamics. One may regard the kinetic pressure of the negative ions within the metal as continually in excess of the pressure of the positive ions; so that in like fields of the double layer, the former escape sooner.

THE TRANSFER IN QUANTA OF RADIATION MOMENTUM TO MATTER

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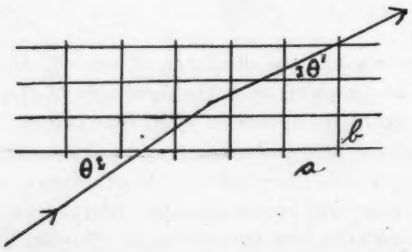
Communicated, March 2, 1923

1. The reflection by a crystal of X-radiation characteristic of the atoms in the crystal itself, which Dr. G. L. Clark and the writer discovered (these PROCEEDINGS, May, 1922 and April, 1923), does not appear to be explainable in a simple manner by the theory of interference of waves. This note describes an attempt to formulate a theory of the reflection of X-rays by crystals, based on quantum ideas without reference to interference laws.

2. The fundamental hypothesis of the theory now presented is that the *momentum* of radiation is transferred to and from matter in quanta, and further, that the laws of the conservation of energy and of momentum apply to these transfers.

3. In order to illustrate the meaning of this hypothesis, let us take a particular example, namely, that of the reflection of an X-ray by a crystal. For the sake of simplicity, let us assume that the axes of the crystal lie



at right angles to each other and take the particular case in which the X-ray strikes the crystal in a direction parallel to one set of principal planes. The problem thus becomes a two-dimensionable one. Suppose

that the distances between parallel planes are a and b, respectively, and let an X-ray of energy $h\nu$ and momentum $h\nu/c$ pass through the crystal at an angle θ with the planes, called x, as represented in the figure. At some point in its path the X-ray may be deflected so as to travel in a direction, making an angle θ' with the x planes. At this point of deflection the X-ray transfers some momentum and energy to the crystal. The mass of the crystal being so large, however, the velocity acquired by it must be very small and, consequently, the energy transferred from the radiation to the crystal may be neglected. We will take up later the case where the X-ray may break up one of the atoms of the crystal, ejecting an electron and, therefore, transferring energy to the atom on that account. Neglecting the amount of energy transferred to the crystal, we may put $h\nu' = h\nu$ and we may consider that the X-ray has the same energy and total momentum after the transfer as before.

The momenta transferred to the crystal in the directions x and y, respectively, are expressed by the following equations:

$$M_x = h\nu/c.(\cos\theta - \cos\theta'), \quad M_y = h\nu/c.(\sin\theta - \sin\theta'). \qquad (1)$$

According to the fundamental hypothesis the momentum M_x transferred to the crystal is to be delivered in quanta. We may write, therefore, M_x proportional to the constant h. Now, let us apply to the problem dimensional reasoning. The momentum has the dimensions ml/t and the constant h has the dimensions ml^2/t. In order, therefore, that both sides of our equation may have the same dimensions, we must divide h by a length. Since this is a crystalline phenomenon the only quantity of importance having the dimensions of a length in the direction of the axis of X is the distance a between the crystal planes. Since any whole number, τ, of quanta may be transferred, we will multiply τ into the quotient of h by a and we reach the conclusion that the momentum M_x must be equal to $\tau h/a$ multiplied by some numerical constant. The equation will take its simplest form if we put this constant factor of proportionality equal to unity. We thus get the equation: $M_x = \tau h/a$. Similarly, $M_y = \tau' h/b$. Another way of looking at these equations is to regard them as peculiar applications to the *transfers* of momenta of the quantum equation, $\int p dq = nh$, expressed in generalized coördinates. Substituting for M_x and M_y in equations (1), we get immediately:

$$h\nu/c.(\cos\theta - \cos\theta') = \tau h/a, \quad h\nu/c.(\sin\theta - \sin\theta') = \tau' h/b. \qquad (2)$$

4. In the above equations τ and τ' represent whole numbers. If $\tau = \tau' = 0$, $\theta' = \theta$, and the incident radiation quantum passes through the crystal without deflection. It will keep on traveling through the crystal until it reaches a point where either τ or τ' differs from 0. Suppose

that τ' differs from 0 at some point, and that τ remains 0, then, from the first of equations (2) it follows that $\cos\theta' = \cos\theta$. θ', however, cannot equal θ, for in this case τ' does not equal 0. Consequently, θ' must equal $-\theta$. This means that the X-ray at the point is deflected downward in a direction making an angle with the x-planes equal to the angle of incidence. In other words, the angle of reflection by the x-planes equals the angle of incidence on them.

Substituting $\theta' = -\theta$ in the second of equations (2) we get:

$$2h\nu/c.\sin\theta = \tau' h/b, \qquad (3)$$

which represents the relation that must exist between ν and θ in order that τ' may differ from zero. Putting $\nu/c = 1/\lambda$, equation (3) reduces to:

$$\tau'\lambda = 2b\sin\theta.$$

This is Braggs' law of reflection of an X-ray by a crystal.

By similar reasoning, if $\tau' = 0$ and τ differs from 0, we deduce the equation:

$$\tau\lambda = 2a\cos\theta,$$

which represents reflection according to Braggs' law from the y-planes. If both τ and τ' differ from 0, the equation obtained reduces to Braggs' equation representing the reflection from a set of planes other than the principal planes. In the case where the axes of the crystal are not at right angles to each other, we apply the law of the transfer of momenta in quanta to the total component of the radiation momentum in the direction of each axis and we equate this component to $\tau h/a$ where a is the parameter of the crystal along the axis. This gives us equations which reduce to Braggs' equation for the reflection from each set of planes, as in the orthogonal problem.

5. The reasoning by which we have deduced Braggs' law of reflection of X-rays by a crystal cannot be considered a logical demonstration. We may regard the reasoning, however, as a means of suggesting equations to be tested by applying them to experimentally determined facts. We know, for instance, that Braggs' law holds to a very high degree of precision. On the other hand, the same may be said of all physical theories. General fundamental assumptions form the basis of every physical theory and, no matter how rigorously we may deduce from them laws and facts to be tested by experiment, the theories, on account of the hypothetical character of the fundamental principles, should always be regarded purely as methods of suggesting the laws to be experimentally tested.

6. In the above discussion of the reflection of X-rays by crystals nothing has been specifically said about wave-lengths or frequencies of vibration, although in order to conform with usage the energy of the incident radiation quantum was put equal to $h\nu$, and in order to compare the formulas obtained with the usual expressions of them, the wave-length, λ, was introduced. We might just as well have called the energy ϵ and introduced it into the equations.

In deducing more general equations for the defraction of X-rays by a crystal, let us follow this procedure. Let us take the axes of x, y and z to coincide with the axes of the crystal, having respectively, the parameters d_1, d_2 and d_3. Denote the direction cosines of the incident X-ray, of energy ϵ, by l, m and n, and those of the deflected ray by l', m' and n'. Then, the momentum of the ray being ϵ/c, we may write the following equations for the amounts of momentum transferred to the crystal by the ray in the directions of the axes x, y and z, respectively.

$$(1 - 1')\epsilon/c = \tau_1 h/d_1, \quad (m - m')\epsilon/c = \tau_2 h/d_2, \quad (n - n')\epsilon/c = \tau_3 h/d_3 \quad (4)$$

where τ_1, τ_2 and τ_3 are whole numbers. In addition to these three equations we have the usual relations between the direction cosines 1, m, and n, and between the direction cosines l', m' and n'.

7. To compare these equations with the forms often used to describe the defraction of rays by a crystal we may put $\epsilon = hc/\lambda$ where λ denotes some parameter connected with the radiation quantum ϵ, but need not be regarded in our present theory as the distance between waves, as in the wave theory. Equations (4) then become:

$$\tau_1\lambda = d_1(l - l'), \quad \tau_2\lambda = d_2(m - m'), \quad \tau_3\lambda = d_3(n - n'),$$

general equations for the defraction of X-rays by a crystal.

8. In the case of the reflection of rays characteristic of the chemical elements in the crystal, the theory becomes more complicated. Here we must consider that a certain amount of the energy of the incident ray goes to produce the emission of an electron from an atom with a certain velocity and we must take into account the transfer of momentum to the atom and the emitted electron, as well as to the crystal. Perhaps the simplest fundamental assumption to make is that the incident quantum of radiation delivers part of its momentum to the atom and the electron on the one hand and quantizes the rest with the crystal as in the foregoing examples. From this idea we obtain the equations

$$\begin{aligned} l\epsilon/c - l'\epsilon'/c &= MV_x + mv_x + \tau_1 h/d_1 \\ m\epsilon/c - m'\epsilon'/c &= MV_y + mv_y + \tau_2 h/d_2 \\ n\epsilon/c - n'\epsilon'/c &= MV_z + mv_z + \tau_3 h/d_3, \end{aligned} \quad (5)$$

where ϵ is the energy of the incident quantum of radiation, and ϵ' the total energy of the secondary radiation, M and m the masses, and V and v the velocities of the atom and electron, respectively. The energy, ϵ', equals the $h\nu$ value of a critical absorption frequency characteristic of the chemical element in the crystal. In the secondary radiation from the atom it is divided into parts, ϵ_1, ϵ_2..., corresponding to several emmission lines in the characteristic X-ray spectrum ($\epsilon' = \epsilon_1 + \epsilon_2 + \ldots$). The terms $\epsilon' l'/c$, $\epsilon' m'/c$ and $\epsilon' n'/c$ represent vector sums of the corresponding momenta.

According to our assumption the incident radiation transfers part of its momentum to the atom and electon without change of direction and we have, therefore, the equations:

$$(\epsilon/c - \epsilon'/c)l = MV_x + mv_x, \quad (\epsilon/c - \epsilon'/c)m = MV_y + mv_y,$$
$$(\epsilon/c - \epsilon'/c)n = MV_z + mv_z. \quad (6)$$

Subtracting these equation from equations (5) we get

$$\Sigma\epsilon_1/c(l - l_1) = \tau_1 h/d_1, \quad \Sigma\epsilon_1/c(m - m_1) = \tau_2 h/d_2,$$
$$\Sigma\epsilon_1/c(n - n_1) = \tau_3 h/d_3. \quad (7)$$

In these equations the first members consist of several terms. In each case the first term is very much larger than the sum of all the others. For example, in the K series of X-rays, the sum of the ϵ's for all the lines in the other series amounts to less than 20% of the value of ϵ for the $K\alpha$ line. In the case of the $K\beta$ line, the sum of the ϵ's other than the $K\beta$ amounts to only about 3.4% of the $K\beta$. For the γ line the sum amounts to a small fraction of 1% of the $K\gamma$. We see, therefore, that we may write the approximate equations

$$\epsilon_1/c(l - l_1) = \tau_1 h/d_1, \quad \epsilon_1/c(m - m_1) = \tau_2 h/d_2, \quad \epsilon_1/c(n - n_1) = \tau_3 h/d_3 \quad (8)$$

for the lines in the K series.

Since terms in equations (7) may be positive or negative, and since the value of a direction cosine can never exceed unity, it follows that l_1, m_1 and n_1, as given by equations (7), lie in the neighborhood and on both sides of certain mean values, given by equations (8). The approximations to the mean values are much closer in the case of the β lines than in that of the α lines, and still closer in the case of the γ lines. The equations (7), therefore, may be interpreted as meaning that the characteristic radiations come off from the crystal in directions approximating to those directions which obey the laws of defraction by the crystal. Further, the $K\beta$ reflection should be more intense and more sharply marked than the $K\alpha$ reflections, and the $K\gamma$ reflections should be still more sharply

marked. Again, in spectra of higher orders the direction cosines have larger values than in spectra of lower orders, and on this account we would expect somewhat more sharply marked reflections in the former than in the latter. It has been shown experimentally by Dr. Clark and the writer, that the characteristic reflections we discovered have precisely these peculiarities; so that our theory accounts for not only the reflections of rays from the crystal that are characteristic of the chemical elements in it but also for their most apparent details.

9. The application of the theory sketched in this note to the reflection, refraction, defraction, etc., of light, leads to interesting conclusions, some of which will now be discussed. The chief problem involved in these applications is the selection of suitable parameters, each having the dimensions of a length, to divide into the action constant, h.

Let us apply the theory to the case of a defraction grating. Let a quantum of radiation of energy $h\nu$ fall upon the grating in a direction making an angle i with the normal, and suppose that it is defracted at an angle r with the normal. Then, taking the components of the momenta in a direction along the surface of the grating perpendicular to its lines, we get the equation

$$(\sin i - \sin r)h\nu/c = nh/d,$$

where the distance, d, between the lines of the grating is the only distance in the direction we are considering that has any meaning. This equation reduces immediately to the ordinary equation for a grating:

$$n\lambda = d(\sin i - \sin r).$$

As a second problem, take the radiation reflected from a thin plate of thickness t. As before, let the radiation quantum fall on the surface at the angle i with the normal and suppose that inside of the plate its direction of motion makes the angle r with the normal. Let the velocity inside of the plate be c', that outside c, and let the length of the plate be l. Taking components of the momentum parallel to the surface of the plate we have the equation:

$$h\nu/c \sin i - h\nu/c' \sin r = nh/l,$$

where l is the only distance in the direction considered that has any meaning. Unless l is very small and comparable with the wave-length of the incident ray, the second term of this equation practically equals 0 for all reasonable values of n, and the equation reduces to

$$\sin i : \sin r = c : c'$$

which is the normal equation for the refraction of light at the surface of two media.

Inside of the plate it may be that the radiation is deflected. Suppose that it is deflected and travels at an angle r' with the normal. Then, taking components parallel to the surface of the plates and in the direction through the plate, we have the equations

$$h\nu/c'(\sin r - \sin r') = n_1 h/l, \quad h\nu/c'(\cos r - \cos r') = n_2 h/t,$$

where t is the only length in a direction normal to the surface of the plate that has any meaning. From the first of these equations we deduce that $r' = r$ or $r' = 180° - r$. In the first case, the quantum passes on through the plate without change of direction inside of it and in the second, it is deflected and comes back through the first surface of the plate at an angle equal to that at which it entered. In other words, it is reflected from the plate at an angle of reflection equal to the angle of incidence. Putting $r' = 180° - r$, we find from the second equation that, $n_2\lambda' = 2t \cos r$, λ' being the wave-length inside of the plate. This is the ordinary equation for the reflection of no light from a thin plate, producing so-called interference. The ordinary equation for the reflection of light may be obtained by adding a half quantum number.

10. In applying the principle under discussion to other problems of interference, the interpretation of the parameter to be used in the equations sometimes becomes very difficult. In general, interference equations are of the form $n\lambda$ equals the difference between two distances, and this may be transformed into an equation representing the difference between two quantities of radiation momentum.

11. According to our present theory the photoelectric effect should obey the law given by the energy equation

$$\epsilon - \epsilon' = \frac{1}{2}MV^2 + \frac{1}{2}mv^2, \qquad (9)$$

in which V is given by equations (6) together with the direction cosine relation. Equation (9) takes account of the energy delivered to the atom as well as that delivered to the electron. The difference between it and Einstein's expression for the photoelectric effect does not amount to much, however, as this difference depends upon the ratio of m to M.

A similar correction should be applied to the equation giving the short wave-length limit of the continuous X-ray spectrum.

MUTUAL ELECTROMAGNETIC MOMENTUM AND ENERGY OF A SYSTEM OF MOVING CHARGES

BY IRWIN ROMAN

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Communicated, March 16, 1923

The momentum and the energy of an electric field due to a system of moving charges differ from the sums for the separate charges by a quantity called the "mutual momentum" or the "mutual energy," respectively. If we consider the system as made up of two charges, e_1 and e_2, and if we select axes of reference in such a way that the charges are at $(a, b, 0)$ and $(-a, -b, 0)$, respectively, for some particular time, the common velocity being along the x-axis, then the components of the mutual momentum will be, in Heaviside units,

$$G_1 = S\int \frac{y^2 + z^2 - b^2}{R}\,d\tau \quad G_2 = S\int \frac{ab - xy}{R}\,d\tau \quad \text{and } G_3 = S\int \frac{-xz}{R}\,d\tau$$

where

$$R = \left\{(x-a)^2 + K^2[(y-b)^2 + z^2]\right\}^{3/2} \left\{(x+a)^2 + K^2[(y+b)^2 + z^2]\right\}^{3/2}$$

$$S = \frac{u}{c^2}\,\frac{K^4 e_1 e_2}{8\pi^2}, \qquad K^2 = 1 - \frac{u^2}{c^2},$$

u being the speed of the system and c that of light, and the integration in τ is to cover the entire field.

The value of G_3 may be found directly and is zero. After a series of simplifying transformations and lengthy reductions, it is found that

$$G_1 = \frac{u}{c^2}\,\frac{e_1 e_2}{8\pi}\,\frac{(K^2b^2 + 2a^2)}{(K^2b^2 + a^2)^{3/2}} \quad \text{and} \quad G_2 = \frac{u}{c^2}\,\frac{e_1 e_2}{8\pi}\,\frac{K^2ab}{(K^2b^2 + a^2)^{3/2}}.$$

Similarly, the mutual energy is found to be

$$U = \frac{e_1 e_2 (K^2b^2 + a^2 + a^2\beta^2)}{8\pi(K^2b^2 + a^2)^{3/2}}, \qquad \text{where } \beta = \frac{u}{c}.$$

Inspection of the results leads to the conclusion that the mutual momentum is parallel to the velocity only in the cases for which the pair of charges

moves parallel or normal to their common line. However the mutual momentum is always in the plane containing the two charges and the direction of motion.

For more than two charges, the mutual effect may be treated as the sum of the effects for all possible pairs, due to the quadratic property of the momentum and energy. The foregoing results have application in the study of "packing effect" in atomic structure.

FURTHER EXPERIMENTS ON THE MASS OF THE ELECTRIC CARRIER IN METALS

BY RICHARD C. TOLMAN, SEBASTIAN KARRER, AND ERNEST W. GUERNSEY

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Introduction.—The production of an electromotive force by the acceleration of a metallic conductor was apparently demonstrated by the work of Tolman and Stewart [*Physic. Rev.*, **8**, 97 (1916); **9**, 164 (1917)], by measuring the pulse of electric current produced by suddenly stopping a coil of wire rotating around its axis. The purpose of the work described in the present article has been twofold. In the first place it seemed desirable to obtain a new demonstration of this production of an electromotive force by the acceleration of a metal, using some method of attack as different as possible from that of Tolman and Stewart, in order to increase our certainty as to the reality of the effect. In the second place it seemed desirable to try to find a method which would eliminate direct electrical connections between moving and stationary parts, and would avoid the sudden stopping of a coil of wire, with the attendant chance of irregular electromotive forces due to buckling or slipping of the wire.

Apparatus.—The apparatus finally used consisted of a copper cylinder $9^1/_8$ inches long, 4 inches outside diameter, and 3 inches inside diameter, oscillating about its axis with a frequency of 18.9 cycles per second. Surrounding this copper cylinder was a coil containing about 60 miles of No. 38 copper wire (diam. 0.1 mm.), which acted as the secondary of a transformer. Connection from this secondary was made through a specially designed three stage amplifier with a vibration galvanometer. The tendency of the electrons in the oscillating copper cylinder to lag behind because of their inertia leads to an electromotive force, the effects of which were finally measured by the deflection of the vibration galvanometer. These galvanometer deflections were then compared with those produced

by the known electromotive force accompanying transverse oscillation of the cylinder in such a way as to cut the earth's magnetic field.

The apparatus was mounted on a massive concrete pier in a special location 150 yards from the nearest electrical circuits, was constructed without the use of magnetic materials, and was driven by air pressure to avoid the disturbances which would have been produced by electrical driving. The axis of the oscillating cylinder was made parallel to the earth's magnetic field in order to reduce accidental effects.

Theory of the Experiment.—The experiments consisted in comparing the electromotive force produced in the cylinder by its rotary oscillation with the electromotive force produced by its transverse oscillation in such a way as to cut the earth's magnetic field. The elementary theory of the experiment may be developed as follows.

If a longitudinal acceleration a is applied to a metallic conductor, the electrons within the conductor will tend to move relative to the main body of the metal as though the conductor were stationary and the electrons were acted on by the force.

$$f = ma \tag{1}$$

where m may be called the "effective mass" of the electron. On the other hand if an electromotive force E is applied to a stationary metallic conductor of length l and uniform cross-section, the electrons within the conductor will be acted on by the force

$$f = Ee/l \tag{2}$$

where e is the charge of one electron. Since the "fictitious" force given by equation (1) and the "real" force given by equation (2) both tend to make the electrons move relative to the main body of the metal, it is evident that they may be equated in order to get an expression for the electromotive force produced by the longitudinal acceleration of a metallic conductor. We obtain, for the electromotive force E, produced in a metallic conductor of length l, by an acceleration a the expression

$$E = mla/e \tag{3}$$

Let us now consider the rotary oscillations of the cylinder around its axis. At any radius r we may evidently write for the instantaneous acceleration, the expression

$$a = 4\pi^2\nu^2\theta_0 r \sin 2\pi\nu t \tag{4}$$

where ν is the frequency of harmonic oscillation and θ is half the angular amplitude of oscillation. Substituting in equation (3) and taking the length of the conductor at the radius in question as $2\pi r$, we obtain

$$E_e = 8\pi^3\nu^2r^2(m/e)\theta_e \sin 2\pi\nu t \qquad (5)$$

as an expression for the electromotive force around a current sheet located in the cylinder at the radius r.

Let us now compare this electromotive force with the electromotive force produced by the transverse oscillation of the cylinder in the earth's field used in calibrating. If θ_c is the half angular amplitude of transverse oscillation, we may write for the maximum flux through a current sheet of radius r, the expression

$$\phi_{\max} = \pi r^2 H \sin\theta_c = \pi r^2 H\theta_c \text{ (for small amplitudes)} \qquad (6)$$

where H is total intensity of the earth's field. Hence for harmonic oscillation of frequency ν, we may write for the electromotive force produced in carrying out the calibration the expression

$$E_c = 2\pi^2\nu r^2 H\theta_c \sin 2\pi\nu t. \qquad (7)$$

Dividing equation (5) by (7) we obtain for the ratio of the electromotive forces produced by the effect and in calibration the expression

$$E_e/E_c = (4\pi\nu/H) \cdot (m/e) \cdot (\theta_e/\theta_c) \qquad (8)$$

or solving for the thing of interest, namely the ratio of the effective mass of the electron to its charge, we obtain,

$$m/e = (H/4\pi\nu) \cdot (E_e/E_c) \cdot (\theta_c/\theta_e) \qquad (9)$$

This is the equation which was used in calculating our experimental results. It will be noted that the radius r of the particular current sheet has dropped out so that E_e/E_c may be taken as the ratio of the total electromotive forces produced by the rotary oscillation and transverse oscillation of the effect cylinder.

In carrying out the actual experiments, a comparison was made of the galvanometer deflections produced by the rotary oscillation of the main cylinder and the transverse oscillation of a much thinner walled calibration cylinder, which was driven with the same frequency as the main cylinder and surrounded by a similar secondary coil. This made it possible to eliminate variability in the behavior of the amplifier by ob-

taining nearly simultaneous readings from the main cylinder and the calibration cylinder. At the close of the experiments a "master calibration" was made comparing the electromotive forces produced by the transverse oscillation in the earth's field of the main cylinder and the calibration cylinders which had been employed. We could than calculate the ratio E_e/E_c which occurs in equation (9) by putting it equal to the ratio of the galvanometer deflections obtained from the main cylinder and from the calibration cylinder multiplied by the ratio determined in the master calibration. The other quantities in equation (9) were determined by direct measurement.

Experimental Results.—In all, eighty-six measurements were made. The average value of m/e in grams per abcoulomb was 5.18×10^{-8}, with an average deviation of 1.33×10^{-8}. The average deviation divided by the square-root of the number of observations was 0.14×10^{-8}.

Conclusion.—It is felt that the work presented above may be regarded as another fairly satisfactory demonstration of the production of electromotive forces by the acceleration of a metallic conductor, and as indicating again that the mass of the carrier in metals is about the same as the mass of an electron in free space. The new work taken by itself alone is perhaps not as convincing as the work of Tolman and Stewart, because of the greater complexity of the apparatus, because of the fact that time did not permit a satisfactory neutralization of the earth's field, and because further developments of the method would be necessary in order to show that the direction of the effect is that predicted on the basis of a mobile *negative* carrier. Our total certainty as to the reality of the effect is, however, greatly increased by the fact that two such widely divergent methods have led to concordant results.

Values of m/e obtained in different ways are given below, in grams per abcoulomb.

m/e in free space	5.66×10^{-8}	(cathode rays)
m/e in copper	6.24×10^{-8}	(Tolman and Stewart)
m/e in silver	6.73×10^{-8}	(Tolman and Stewart)
m/e in aluminum	6.50×10^{-8}	(Tolman and Stewart)
m/e in copper	5.18×10^{-8}	(Tolman, Karrer and Guernsey)

It is evident that our data are not yet accurate enough to determine whether the mass of the electron in a metal is precisely the same as that in free space or not.

A more complete account of the experimental work containing a discussion of the sources of error in the work will be published in the *Physical Review*. The investigation is being continued at the California Institute of Technology.

REMOVAL OF THE BLOCK TO SELF-FERTILIZATION IN THE ASCIDIAN CIONA

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The eggs of Ciona intestinalis found on the Atlantic and Pacific coast of this country cannot be fertilized, as a rule, by sperm of the same individual. A similar phenomenon has long been known in flowering plants. In the latter case it has been shown that the block is due to factors in the pistil that retard the growth of the pollen tube; or else failure to self-fertilize is due to the absence of factors that cause an acceleration of growth in cross-fertilization. In Ciona the nature of the block was unknown despite many attempts to determine it. During the past summer at Woods Hole I have succeeded in bringing about self-fertilization in Ciona by the simple process of freeing the egg from its membranes. The eggs were taken from the oviduct, put into sea water in a flat bottomed watch glass, and by means of two very fine needles the membrane around the egg was torn open. Sometimes the entire egg squeezed out of the slit, sometimes only a part of it pushed out. In either case the extruded protoplasm rounded up into a sphere.

Sperm was taken from the vas deferens of the same individual and diluted. A small amount of the sperm-suspension was added to the water containing the naked eggs and egg-fragments. Most of the eggs and fragments segmented in the course of an hour. The first cleavage was equal; the second equal or nearly equal, also the third. These divisions had every appearance of normal cleavage. Later stages were observed, but not carefully followed.

The same sperm-suspension was added in equal amounts to the eggs of the same individuals that had not been opened and were therefore still surrounded by their membranes. Not one of the eggs divided.

It is obvious from these results that self-fertilization in Ciona is blocked either by the membrane, or by the follicle cells (these stand like a palisade over the outer surface of the egg membrane) or by the test-cells (that lie scattered between the surface of the egg and the membrane), or by some secretion produced by one or by both of these surrounding layers of cells. That the block is not caused by the membrane is evident, since sections of eggs, inseminated by their own sperm, show that the spermatozoa pass to the inside of the membrane. Removal of the follicle cells by shaking them off had shown that such eggs cannot be fertilized. It follows that the block must be caused by the test-cells or by some substance produced by them.

It had been known for some time that the test-cells are derived from maternal tissue. They are not budded off from the egg as some of the earlier observers had claimed. The test-cells stand, therefore, in much the same relation to the spermatozoa as does the maternal tissue of the pistil of plants to the pollen tube. Their secretion must be supposed either to bring the sperm to rest, or to interfere in some other way with the union of the sperm with the egg.

In self-sterile plants it has not been possible to demonstrate whether the pollen could fertilize the egg-cell if it reached it. In Ciona the results here recorded demonstrate that there is no difficulty in self-fertilization if the surrounding cells and membranes are removed. It is true that some self-sterile plants will occasionally set seed at the end of the season, (as shown by East) owing in all probability to the weakening of the block; but such results do not exclude the possibility that the egg itself may have changed. It is interesting, therefore, to find that eggs of Ciona, that can not be self-fertilized while in the membrane, can be self-fertilized if the surrounding cell-envelopes are removed. It seems probable that here the block slows down the spermatozoa or changes their mode of swimming. In plants, on the other hand, East suggests that there is an actual acceleration of the pollen tube in cross-fertilization. In Ciona there is no need for such an hypothesis, since eggs removed from their membranes are as promptly self-fertilized as are the same eggs cross-fertilized with membranes intact.

I have suggested elsewhere that in the self-sterility of Ciona we are dealing with a genetic problem. The present results indicate (as I had suggested) that this relation involves a reaction between maternally derived substances (that have the same genetic inheritance as the cells from which the spermatozoa are derived) and their "own" spermatozoa. In other words, self-sterility in Ciona is not a case of selective fertilization, if by this term we means a selective reaction between the egg and sperms themselves.

The method of obtaining fragments by tearing the membrane will make it possible to study the development of egg-fragments of the unfertilized ascidian egg. A comparison of the development of such fragments with the highly specialized type of development shown by the isolated blastomeres of these eggs should give an opportunity to find out how early the mosaic character of the cleavage is initiated. It is my purpose to examine this question, if possible, this summer.

ON RIEMANN SPACES CONFORMAL TO EINSTEIN SPACES

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1. When two Riemann spaces are so related that the line element of one is merely a multiple of the line element of the other they are said to be *conformal*. Let an n-dimensional Riemann space V_n be given by its line element

$$ds^2 = g_{\alpha\beta}\, dx_\alpha\, dx_\beta, \qquad |g_{ij}| \neq 0;$$

it seems natural to inquire whether or not V_n is conformal to an *Einstein* space, that is, a space satisfying Einstein's "equations of gravitation" (see § 2). The writer has given a complete answer to this inquiry in a paper which has been sent to the Mathematische Annalen. A necessary and sufficient condition that V_n be conformal to some Einstein space is given and various applications of this condition are then made. The present note contains a few of the more striking results, especially those relating to four-dimensional ("relativity") spaces. The details of the proofs will be found in the paper referred to.

2. Any Riemann space $\overline{V}_n$ conformal to V_n can have its line element put in the form:[1]

$$d\bar{s}^2 = \bar{g}_{\alpha\beta}\, dx_\alpha\, dx_\beta$$

where

$$\bar{g}_{ij} = e^{2\lambda} g_{ij},$$

λ being a function of $x_1, \ldots, x_n$. Dashes will be used to designate all quantities belonging to $\overline{V}_n$.

The "gravitational equations" for $\overline{V}_n$ alluded to in § 1 we take in the following, most general, form:

$$\overline{R}_{ij} = \frac{1}{n}\, \overline{R} g_{ij}, \qquad (2.1)$$

$\overline{R}_{ij}$ being the contracted Riemann tensor and $\overline{R}$ the scalar curvature of $\overline{V}_n$; $\overline{V}_n$ is thus an *Einstein* space if and only if (2.1) holds. When $n = 2$ (2.1) is always satisfied; and an Einsteinian V_3 is of constant Riemann curvature,[2] hence we assume $n > 3$. Then $\overline{R}$ is a constant.

We find that (2.1) is satisfied if and only if λ is a solution of the following equations,

$$\lambda_{ij} - \lambda_i\lambda_j + \wedge g_{ij} = L_{ij}, \tag{2.2}$$

$$\wedge_{(x)} = \frac{1}{2} g^{\alpha\beta}\lambda_\alpha\lambda_\beta - \frac{\bar{R}}{2n\,(n-1)}\, e^{2\lambda}. \tag{2.3}$$

Here $\lambda_i = \partial\lambda/\partial x_i$; λ_{ij} is the second covariant derivative of λ with respect to V_n, and

$$(n-2)L_{ij} = -R_{ij} + \frac{1}{2(n-1)} Rg_{ij}.$$

From (2.2) and (2.3) we derive

$$\lambda^\alpha C_{\alpha ijk} \equiv \lambda_\alpha C^\alpha_{ijk} = S_{ijk} \tag{2.4}$$

where the "conform curvature" tensor C_{ijkl} is built out of the Riemann tensor R_{ijkl} thus:

$$C_{ijkl} = R_{ijkl} + g_{il}L_{jk} - g_{ik}L_{jl} + g_{jk}L_{il} - g_{jl}L_{ik},$$

and

$$S_{ijk} = L_{ij/k} - L_{ik/j},$$

$L_{ij/k}$ being the covariant derivative of L_{ij}.

From (2.4) equations similar to (2.4) can be found, they are all linear in λ_i and $\wedge_x$ *and must be compatible if* V_n *can be mapped conformally on an Einstein space.*

3. The results are particularly entertaining when V_n is itself an Einstein space. Then V_n can of course be mapped conformally on an Einstein space (namely itself) by putting λ = const.; we call such a map a *trivial* map. Theorems analogous to the following are readily obtained:

If an Einstein space can be mapped non-trivially on an Einstein space with non-vanishing scalar curvature it can be so mapped on an Einstein space with zero scalar curvature.

4. The most satisfactory results are those found for the dimensionality $n = 4$. We begin by establishing the following lemma.

When $n = 4$ *the equation* $\mu^\alpha C_{\alpha ijk} = 0$ *implies either*

$$C_{ijkl} = 0, \quad (4.1), \qquad \text{or } \mu^{(i)} = 0, \quad (4.2)$$

This is proved by introducing coördinates such that at any pre-assigned point the components of C_{ijkl} take a certain simple form—most of them-

being zero; the normalization thus achieved is essentially due to Kretschmann[3] and is also used by Bach.[4]

When (4.1) holds $V_n (n > 3)$ is conformal to Euclidean space ("conform-euclidean"),[5] if (4.2) is true then λ_i is uniquely determined from (2.4)—if these equations have a solution at all—hence we conclude that

A V_4 which is not conform-euclidean can be mapped conformally on at most one Einstein space and the mapping can be accomplished (if at all) in one way only, provided we neglect a change of scale.

In particular, if V_4 is an Einstein space to begin with it is conform-euclidean only if it is of constant Riemann curvature, consequently

The only Einstein 4-space which can be conformally mapped on Einstein spaces in a non-trivial manner are those of constant Riemann curvature (spherical spaces).

This last theorem is proved by Kasner[6] for two special cases:

(*a*) V_4 is conform-euclidean as well as Einsteinian,

(*b*) V_4 is defined by the Schwarzschild "solar field" line element.

That an Einsteinian V_n (for any $n > 3$) is necessarily of constant Riemann curvature whenever it is conform-euclidean is proved by Schouten and Struik.[2]

[1] Einstein, A., *Berlin, Sitzber. Ak. Wiss.*, 1919 (349–356).

[2] Schouten, J. A. and Struik, D. J., *Amer. J. Math.*, **43**, 1921 (213–216).

[3] Kretschmann, E., *Ann. Physik.*, **53**, 1917 (593–596).

[4] Bach, R., *Math. Zeitschr.*, **9**, 1921 (120–121).

[5] Schouten, J. A., *Ibid.*, **11**, 1921 (58–88).

[6] Kasner, E., *Amer. J. Math.*, **43**, 1921 (20–28) and (219–220); *Math. Ann., Leipzig*, **85**, 1922 (227–236).